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REVIEW ARTICLE

Impact of climate change on weeds in agriculture: a review

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Abstract Over the past decades, climate change has induced transformations in the weed flora of arable ecosystems in Europe. For instance, thermophile weeds, late-emerging weeds, and some opportunistic weeds have become more abundant in some cropping systems. The composition of arable weed species is indeed ruled by environmental conditions such as temperature and precipitation. Climate change also influences weeds indirectly by enforcing adaptations of agronomic practice. We therefore need more accurate estimations of the damage potential of arable weeds to develop effective weed control strategies while maintaining crop yield. Here we review the mechanisms of responses of arable weeds to the direct and indirect effects of climate change. Climate change effects are categorized into three distinct types of shifts occurring at different scales: (1) range shifts at the landscape scale, (2) niche shifts at the community scale, and (3) trait shifts of individual species at the population scale. Our main conclusions are changes in the species composition and new species introductions are favored, which facilitate major ecological and agronomical implications. Current research mainly considers processes at the landscape scale. Processes at the population and community scales have prevalent importance to devise sustainable management strategies. Trait-climate and niche-climate relationships warrant closer consideration when modeling the possible future distribution and damage potential of weeds with climate change.

Keywords Agroecology · Arable biodiversity · Weed management · Weed control · Weed species composition · Functional trait · Ecological niche · Central Europe

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1 Introduction

Over the past decades, some distinct transformations have been recorded in the weed flora of arable ecosystems in Europe (e.g., Schroeder et al. 1993; Sutcliffe and Kay 2000; Weber and Gut 2005; Fried et al. 2008; Novak et al. 2009; Potts et al. 2010; Andreasen and Streibig 2011; Kolarova et al. 2013; Salonen et al. 2013). For example, increasing numbers of thermophile weeds such as *Amaranthus retroflexus* (Fig. 1) and *Abutilon theophrasti* became established in more northern

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Fig. 1 Photo of *Amaranthus retroflexus* growing within maize

Fig. 2 Photo of wild *Sorghum halepense* as one profiting weed. Plants typically grow larger than maize plants

areas, including exotic and potentially invasive species such as *Panicum dichotomiflorum* and *Datura stramonium* (Guillerm et al. 1990; Breitsameter et al. 2014). Some late emergers such as *Chenopodium* spp. and millet weeds such as *Echinochloa* spp., *Setaria* spp., *Digitaria* spp., and *Sorghum halepense* (Fig. 2) have expanded their distribution range (Mehrtens et al. 2005; Otte et al. 2006). Weeds that have formerly been of minor importance have regionally become highly relevant species ("chance species," see Baessler and Klotz 2006). These "upstarters" include species such as *Stellaria media*, *Geranium* spp., several species of the subfamily Polygonoideae, and some crucifer (Brassicaceae) weeds (Peters et al. 2009; Meissle et al. 2010). As a result, arable ecosystems and agronomy are faced with the need to adapt weed control to these altered conditions.

Climate change will cause further alterations in the arable weed species composition. Predicted rates of climate change exceed any of the observed rates of change of the past 420,000 years (Petit et al. 1999; Loss et al. 2011). As a result, climate change may become one of the most important determinants for the distribution of arable weeds (Pautasso et al. 2010). Climate change leads to altered environmental conditions such as altered temperatures and precipitation that directly affect arable weeds. Climate change also influences weeds indirectly by enforcing adaptations of farming methods such as crop choice, sowing time, harvesting date, and other agronomical practices to these alterations (Fleming and Vanclay 2010).

In this review, we present three distinct kinds of shifts (range shift, niche shift, trait shift) acting at landscape, community, and population scales as the basic processes underlying current changes in the arable weed flora. We further highlight interrelations among these individual processes at different scales and apply existing ecological knowledge from natural and seminatural ecosystems to arable ecosystems. Yet, in contrast to the ecological concept of regime shifts, our concept of shifts represents small and gradual changes in the structure and function of the arable ecosystem (Scheffer et al. 2001; Brock et al. 2008; Samhouri et al. 2010). Finally, we point out areas for further research targeted at improving estimations of possible future effects of climate change on arable ecosystems that will help to devise management options to meet the challenges resulting from climate-mediated shifts.

2 Direct effects of climate change on weeds

Climate change involves rising temperatures (Tubiello et al. 2007; Gillett et al. 2011) and altered precipitation patterns,

which also increase the probability for summer droughts in Europe (Bloomfield et al. 2006; Lobell and Burke 2008; Robinson and Gross 2010). Weeds are influenced by these altered abiotic conditions (Dukes et al. 2009; Singer et al. 2013). For example, wetter and milder winters are likely to increase the survival of some winter annual weeds, whereas warmer summers and longer growing seasons may permit thermophile summer annuals to grow in regions further north (Bloomfield et al. 2006; Walck et al. 2011; Hanzlik and Gerowitt 2012).

Furthermore, climate change is predicted to result in a higher frequency of extreme weather events such as heavy storms, summer droughts, and extreme cold spells (Diaz et al. 1999; Tubiello et al. 2007; Jentsch et al. 2009; Coumou and Rahmstorf 2012). As a result, seasonal fluctuations of the local climate are likely to occur more frequently and with larger amplitudes (Walther et al. 2002; Jentsch et al. 2009). Weeds with low phenotypic plasticity regarding these climatic changes are likely to decline. Both extreme weather events and rapid climatic changes disrupt the stability of arable ecosystems and increase the level of disturbance (Dukes and Mooney 1999).

Due to human actions, the concentration of atmospheric greenhouse gases such as methane (CH_4), nitric oxides, sulfur dioxide (SO_2), ozone (O_3), carbon dioxide (CO_2), and gaseous water (H_2O) will rise in the future (Patterson 1995). The effect of increased levels of CO_2 on plants has been intensively studied (e.g., Zangerl and Bazzaz 1984; Ziska 2003; Rogers et al. 2008). In brief, C_3 plants benefit from rising CO_2 levels physiologically. As several studies suggest, however, rising temperatures can override the stimulating effects of CO_2 on photosynthesis (the Calvin cycle) of C_3 plants (Batts et al. 1997; Morison and Lawlor 1999). The negative effect of higher temperatures on C_3 plants depends on the norm of reaction of the plant species and the prevailing environmental conditions (Patterson 1995). By contrast, photosynthesis of C_4 plants is more effective compared to that of C_3 plants at higher temperatures, but C_4 photosynthesis is usually not affected by atmospheric CO_2 enhancement (Carter and Peterson 1983; Ziska 1997).

3 Indirect effects of climate change on weeds via land use and management

Arable ecosystems are defined and shaped by human interference, which differentiates them from any natural and seminatural ecosystem. Weeds in arable ecosystems are adapted to ecological idiosyncrasies resulting from the various farming practices (Grime 1977). Land use and management practices are influenced by climatic changes (Fleming and Vanclay 2010). As weeds are closely associated with the cropping system (Pysek et al. 2005; Andreasen and Skovgaard 2009; Cimalova and Lososova 2009; Gunton et al. 2011), climate change has an indirect influence on the occurrence of weeds via crop management and land use.

The effects of climate change on arable ecosystems are widely discussed in literature (e.g., Sala et al. 2000; Fuhrer 2003; Pautasso et al. 2010). Yet, just a few papers cover the effects of climate change on weeds in relation to specific crops (Patterson et al. 1984; Alberto et al. 1996; Tungate et al. 2007). To assure harvest in the face of climate change, farmers adapt cropping systems and management measures, for instance, by implementing different crop rotations, crop sowing dates, irrigation, and tillage methods (Kaukoranta and Hakala 2008; Fleming and Vanclay 2010; Daccache et al. 2012). Farmers are also likely to choose new, climatically suited crops or cultivars that are better adapted to warm and dry conditions (Bloomfield et al. 2006; Tokatlidis 2013). Extreme weather events in the future will probably set yield at higher risks, which may lead to an increase in pesticide usage and fertilizer input (Baessler and Klotz 2006; Lososova et al. 2006). Arable land use is also projected to be expanded to cover less fertile soils while becoming more uniform across the landscape (Olesen and Bindi 2002). Ultimately, politics (e.g., decisions, legislative framework, public money) and market economics (e.g., demand for commodities, private and corporate investment) additionally influence agronomic practices (Olesen and Bindi 2002).

Rising atmospheric CO_2 is likely to alter the competition between weeds and crops; yet, the outcome depends on the individual set of conditions. On one hand, some weeds may be able to evolve successful attributes more rapidly than crops due to their high genetic variation and plasticity (Baker 1965). On the other hand, breeding of CO_2-efficient crops such as wheat, maize, or soybean is likely to advance in the future (Ziska et al. 2005; Tokatlidis 2013). Elevated CO_2 levels and warmer and wetter conditions can also alter the efficiency of certain herbicides by influencing the physiology of plants (Poorter and Navas 2003; Dukes et al. 2009).

4 General principles of the weeds' reactions

The effects of changing climatic conditions impact arable weeds in various ways. In order to persist in a local habitat, species have to respond to the changes of the environment (Woodward and Cramer 1996). These responses lead to shifts, which act at distinctive scales (see below). Generally, plant species have three options to avoid extinction (Lavorel and Garnier 2002; Pautasso et al. 2010):

1. *Migration* with a favorable climate, which leads to alterations of the distribution of weeds—a process called *range shift*. For migration, weeds need to possess appropriate propagule dispersion mechanisms. In arable

ecosystems, this is often also provided by human actions (Kubisch et al. 2013). Range shifts act at the landscape scale (Jump and Peñuelas 2005).

2. *Acclimation* to changes in climate conditions basically refers to the response of species within their phenotypic plasticity without evolutionary adjustments (Pearman et al. 2008). These responses can be divided into tolerance and avoidance of climatic changes that lead to performance beyond the species' ecological optimum (Grime and Hodgson 1987; Lavorel and Garnier 2002). As a consequence, the fitness and the competitive ability of the weeds are either reduced or enlarged (Barrett 2000). Consequently, the realized niche is being altered, which leads to *niche shifts*. They act at the community scale and can be determined visually as composition shifts.
3. *Adaptation* to changes in climate conditions, which is often associated with the evolution of new properties or with the optimization of existing ones (Harlan and de Wet 1965; Carroll et al. 2007; Tungate et al. 2007). These individual biological adaptations of weeds, which are driven by natural selection, result in *trait shifts*. They become apparent at the population scale, but are brought about by morphological, physiological, and genetic processes at the individual plant scale.

Our literature search for this review revealed that agricultural research with regard to climate change has mainly considered processes at the landscape scale (Table 1). However, in most cases, range shifts are accompanied by processes at the community and population scales (Hulme and Barrett 2013; Ebeling et al. 2008). Especially trait shifts have infrequently been linked to climate change so far (Table 1). Moreover, most existing studies rely on literature or on meta-analysis of data (Table 1).

In order to understand the processes underlying the current transformations of the arable ecosystems, a more comprehensive knowledge of shifts at all scales is needed. In the following, we explain the ecological basis of these individual types of shifts. By highlighting some examples from current research, we relate them to the context of the responses of arable weeds to climate change. For reasons of an initial categorization, we present the different types of shifts as separate processes. However, it needs to be kept in mind that several shifts can be intermingled across the distinct scales they are acting at.

5 Range shifts

Range shifts represent the transformation of the distribution area of species and occur at the landscape scale, i.e., at a geographical area extending from several arable fields up to few hundred kilometers (Pearson and Dawson 2003; Petit et al. 2011). With recent climate change, plant species are expected to track the climate favorable to their growth (Jump and Peñuelas 2005). This is well investigated and documented for Europe (Cimalova and Lososova 2009; Silc et al. 2009; Walck et al. 2011; Hanzlik and Gerowitt 2012). Rising temperatures can cause species range boundaries to be moved further toward the poles (Walther et al. 2002). As a result, many C_4 weeds such as *A. retroflexus*, *Setaria* spp., *Digitaria* spp., *P. dichotomiflorum*, and *S. halepense* are expected to extend their distribution range to locations further north (Fausey and Renner 1997; Weber and Gut 2005; Clements and Ditommaso 2011) (Figs. 1 and 2). Presumably, increased levels of precipitation during winter will additionally shift the range of many weed species moderately eastward in Europe (Skov and Svenning 2004; Bergmann et al. 2010). The effect of climate change on the number of weed species is likely to be more pronounced in northern regions of Europe, as the number of weeds is lower there than in southern regions (Holzner and Immonen 1982; Fried et al. 2008).

Opportunistic weed species possess the ability to track climate change by means of sophisticated dispersal and superior adaptation capabilities (Chapin et al. 1996; Bergmann et al. 2010; Pautasso et al. 2010). Human-promoted propagule dispersion via transport routes and trade can act as a trigger with certain species such as *Ambrosia artemisiifolia* (von der Lippe et al. 2013; Milakovic et al. 2014), which is not always clearly distinguishable from climate-related mechanisms. Possibly due to an interaction of human actions and climatic changes, the maize weeds of the genus *Setaria* (Douglas et al. 1985; Wang and Dekker 1995) and *A. theophrasti* (Andersen et al. 1985; Warwick and Black 1986) have extended their range to Northern America.

If climate change occurs too rapidly, some species may be unable to track the climate to which they have adapted over time (Jump and Peñuelas 2005; Broennimann et al. 2006). In addition, species whose propagule transport mainly relies on biological dispersal mechanisms, habitat fragmentation, and dispersal barriers like mountains may also prevent range shifts (Bazzaz 1996; Grime 1997). This mainly appears to be the case for locally rare species such as *Scandix pecten-veneris* and *Silene noctiflora* (Lososova et al. 2006; Hyvönen et al. 2012).

In order to sustain a population in a novel habitat, weeds must persist after they have become established (Weiher et al. 1999; Smith et al. 2011). As a consequence, range shifts are often accompanied by natural selection leading to genetic and evolutionary adjustments to the novel environments (Levin 2009; Lavergne et al. 2010; Richardson et al. 2013). These evolutionary processes result in trait shifts (see Section 7). The level of evolutionary adaptations is highest at the expanding front (the colonizing edge) and at the boundary of the range (Angert et al. 2011; Doxford and Freckleton 2012).

Table 1 References on shifts of weeds in arable ecosystems with focus on Central Europe. References are sorted by shift type, community, and geographical area

Shift type	Plant community	Research related to climate change?	Geographical area	Method of projection	Weed species	Main results	References
Range shift	Arable	Yes	Europe	Modeling	Meta study on 25 species	Range size of arable weed species will increase or decrease under future climate change, drastic changes in the establishment of arable weeds, a species gain in northern parts of Europe and a species loss in southern parts	Hyvönen et al. (2012)
	Arable and ruderal	Yes	North America	Modeling	Meta study on 9 species	Comparison study on the modeling of two habitat suitability datasets, incorporation of expert knowledge into models, distribution models of invasive species should include abundance and occurrence data	Bradley (2013)
	Ruderal	Yes	North America	Experiment	*Bromus tectorum*	Ecological shift from snow to rain in late winter facilitates range shift of *B. tectorum*	Concilio et al. (2013)
	Various, including arable and ruderal	Yes	UK	Modeling	Meta study on 1,131 native, 140 archaeophytic, and 145 neophytic species	Land use change can be a driver of species distributions under future climate change, some species are more affected by climatic changes, others more of land use changes	Hulme (2008)
	Various	Yes	Great Britain	Modeling	Meta study on 4 species	Presentation of a model framework for studying the effects of climate and land-cover changes on species distributions, incorporating land use data significantly improves purely climate-driven prediction models	Pearson et al. (2004)
	Various	Yes	British Isles	Modeling	Meta study on 40 species	Rare species respond distinctly to climate change, range shift northward/poleward often not possible for rare species due to drastic changes, nature conservation measures needed to sustain biodiversity under climate change	Berry et al. (2007)
	Various	Yes	Germany	Modeling	Meta study on 845 species	Rather large changes in the arable flora under climate change conditions, species with small ranges will be vulnerable to climate change, generally a species loss in southern parts of Germany and a moderate species gain in northern parts	Pompe et al. (2008, 2011)
	Various	Yes	Australia	Modeling	Meta study on 584 species	Connecting range shifts with nature conservation measures increases robustness of range shift predictions	Summers et al. (2012)
Niche shift	Arable	Yes	North America, Europe	Modeling	*Centaurea maculosa*	A shift of the climatic niche occurred between native and nonnative habitats, climate matching may not be enough to predict full extent of range expansion under climate change	Broennimann et al. (2007)
	Ruderal	No	France and Australia	Experiment	Mixture of 6 annual grasses, 6 annual legumes, and 6 annual composites	Survival and fitness of invaders are influenced by the functional connections in nonnative habitats, climate conditions in nonnative habitats have less effects than functional connections between residing species	Lavorel et al. (1999)
	Ruderal	Yes	UK and America	Statistical	Meta study on 19 species	Trait-environment relationships, combined niche and trait shift (first flowering date) in nonnative habitats, explain the potential for future range shift of the species	Hulme and Barrett (2013)
	Mainly ruderal	Yes	Worldwide	Modeling	Meta study on 50 species	Niche conservatism, climate-induced niche shifts are sometimes rare among colonizers and invaders, because species often tend to	Petitpierre et al. (2012), Webber et al. (2012)

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Table 1 (continued)

Shift type	Plant community	Research related to climate change?	Geographical area	Method of projection	Weed species	Main results	References
						occupy climate conditions close to native conditions	
	Various	Yes	Germany, Central Europe	Modeling	Meta study	Modeling of regions with suitable niches and species pools under future climate conditions revealed a change toward warmth- and drought-adapted species that are currently distributed in southern regions of Europe	Bergmann et al. (2010)
	Subalpine	Yes	Scandinavia	Experiment, modeling	*Vaccinium myrtillus*, *V. idaea*, *V. uliginosus*	Ontogenetic niche shifts due to climatic effects can exacerbate the correctness of migration modeling	Auffret et al. (2010)
	Ornamental	Yes	Northern Hemisphere (Eurasia, North America)	Experiment, modeling	*Buddleja davidii*	Significant variation in frost resistance among populations limits niche shifts, but not range shifts under future climate conditions	Ebeling et al. (2008)
Trait shift	Arable	Yes	Finland	Statistical	Meta study	There is no universal trait or set of traits that explain the success of weeds in arable ecosystems, the influence of climate depends on the species' habitat preferences	Jauni and Hyvönen (2012)
	Arable	No	France	Statistical	Meta study on 274 species	Invasive and exotic weeds tend to have traits related to high growth rate, high biomass accumulation, and nutrient-rich soils when climate is similar to that in their native habitat	Maillet and Lopez-Garcia (2000)
	Arable	No	Central Europe, Czech Republic	Statistical	Meta study on 381 species	Linking species traits to regional abundance, most successful arable weeds tend to have traits related to low temperatures, shade tolerance, high growth, high reproduction, and fertile soils	Lososova and Simonova (2008)
	Arable	Yes	Central Europe	Monitoring, review	Meta study	Review of species traits along a temperature gradient that changed over a 40-year period	Walck et al. (2011)
	Arable	No	North America, Canada	Monitoring, statistical	*Abutilon theophrasti*	Species differ genetically between populations of geographically different regions, which has implications for trait differentiation and range shift capabilities	Andersen et al. (1985), Warwick and Black (1986)
	Arable	No	North America, South Canada	Monitoring, review	*Setaria* spp.	Northward/poleward spread of several *Setaria* species due to trait shifts maybe connected to climate	Dekker (2003)
	Arable	Yes	North America	Experiment	*Brassica rapa*	Rapid climate change such as a 5-year drought event can facilitate evolution of multiple life-history traits	Franks and Weis (2008)
	Arable	No	North America	Statistical	Meta study on more than 40 species	Community assembly depends on the traits of residing species, an altered timing of tillage leads to differently assembled communities	Smith (2006)
	Various	Yes	Europe	Statistical	Meta study on 542 species	Phenology of plants advanced during 1971–2000 and will further advance under future climate change	Menzel et al. (2006)
Damage shift	Arable	Yes	UK	Modeling	*Alopecurus myosuroides*	Although the weed distribution is predicted to remain similar under climate change, the damaging niche is reduced due to drought events and higher atmospheric CO_2 concentrations	Stratonovich et al. (2012)
	Arable	Yes	America	Modeling	*Abutilon theophrasti*, *Sorghum halepense*	The damaging niche of weeds shifts geographically alongside climate change and range transformations of cropping systems	McDonald et al. (2009)

6 Niche shifts

In ecosystems, every species occupies an ecological niche. In this review, we follow the niche concept of Hutchinson (1957). Herein, the fundamental niche is defined as an *n*-dimensional hypervolume, with each dimension representing the environmental resources required by species for survival (Colwell and Rangel 2009). Limited environmental resources and interspecific competition by other organisms reduce the size of the fundamental niche of a species to the realized niche. Along with the niches of other species, all realized niches are arranged in the niche pool in a particular habitat (Silvertown 2004; Fried et al. 2010). The size of the niche pool defines the maximum space available to be occupied by niches.

Changing climatic conditions lead to a transformation of the size and the shape of the niche pool, which affects the species niches inside the pool and, consequently, causes alterations in the community (Chapin et al. 1996). There are very few examples of climate-mediated niche shifts in arable ecosystems. Broennimann et al. (2007) demonstrated that *Centaurea maculosa* actively realized a niche shift. This species was introduced from Europe to Northern America and extended its niche by adapting certain traits. Like in this example, niche shifts are often accompanied by other shifts.

Most agronomic actions are designed to remove weeds from the local species pool (Holzner and Immonen 1982). As a result, farming practices—which vary depending on climate—cause disturbance to the system and influence the construction of niches by creating niche gaps (Clements et al. 1994; Eriksson 2013). Niche gaps also result from disturbance as caused by extreme climate events such as extreme wind, frost, rain, and other mechanical disruptions. Niche gaps directly affect the abundance and cover of weeds due to the removal of plants caused by disturbance (Booth and Swanton 2002; Nogues-Bravo 2009). This process is often followed by a temporary increase in the availability of nutrients and a reduction in competition (Stohlgren et al. 1999). Ecologically, niche gaps represent empty space in the niche pool. Dekker (2003) describes niche gaps as "opportunity space" for exotics and invaders. Yet, niche gaps as caused by extreme weather events can also be an additional opportunity for weeds to emerge (Hobbs and Huenneke 1992). Thus, niche gaps most often become apparent by relatively high fluctuations between species or high introduction rates of species (MacArthur 1955).

Yet, most disturbances disrupt the structure of the ecosystem inconspicuously by disorganizing or removing ecological linkages between species (MacArthur 1970; Clements et al. 1994). Weed species are intermingled with each other within the local community to a varying degree. As a result, they react on the community level rather than as single entities (Weiher et al. 1999). Still, the processes linking the responses of weed communities to plasticity, competition, and disturbance are not well understood so far (Post et al. 2001; Nogues-Bravo 2009; Estrella et al. 2009).

It has been argued that each kind of disturbance has stronger effects in less diverse ecosystems and that these ecosystems can be more prone to the introduction of arable newcomers (Drake 1990; Walther et al. 2002). In arable ecosystems with diverse weed communities, more weed species are present that can fill niche gaps and prevent the establishment of new species (Booth and Swanton 2002). In less diverse arable communities, the fewer resident species occupy empty niche space more slowly and less efficiently after disturbance (Rejmanek 1989). Due to their large niche size and few, but very stable linkages, "keystone species" exert a large effect on the community. If a keystone species is removed, community function will be changed drastically (Booth and Swanton 2002). Weed communities with a history of frequent herbicide treatments often lack keystone species, which lead to less stable arable communities that are often prone to the establishment of arable newcomers and invasive species (Fox and Fox 1986). Invaders often exert symptoms of becoming new keystone species themselves (Guillerm et al. 1990; Clements and Ditommaso 2011).

The underlying processes of niche shifts of arable weeds are most often invisible and difficult to quantify. However, as niche shifts usually lead to an altered dominance of species in the community, they often become apparent as changes in the composition of arable weed species (Chapin et al. 2000; Booth and Swanton 2002). Composition shifts can be determined as they result from changes in the abundance and the population structure of weed species (MacArthur 1955; Elton 1958; Harlan and de Wet 1965; Singer et al. 2013). For example, the current species pool in Germany (Pompe et al. 2008; Bergmann et al. 2010) and other European countries (Ihse 1995; Menzel et al. 2006; Hyvönen 2011; Potts et al. 2010) already indicates a change toward weeds that are adapted to warm and dry summer conditions.

7 Trait shifts

Traditionally, a plant trait represents a measurable attribute of a species (Raunkiaer 1934; Weiher et al. 1999). In recent decades, efforts have been made to devise functional groups of attributes with relation to ecological factors or resources (Grime 1977; Craine et al. 2001; Lavorel and Garnier 2002; Gunton et al. 2011). The ecosystem supplies the plant with nutrients, energy, atmospheric gases, and water. Only those species prevail that possess the appropriate sets of (functional) traits suited for making use of the resources given in a certain area (McIntyre et al. 1999). The trait set of a species is the basis of its functional relationship to the environmental resources and to other species within the ecosystem. Recently, multivariate analyses help in determining these functional

connections (Lososova et al. 2006; McGill et al. 2006; Fried et al. 2008; Jauni and Hyvönen 2012). A changing climate influences the supply of resources, and as a consequence, it alters the functional connections of traits (Diaz et al. 1998; Jauni and Hyvönen 2012). Climate change hence selects those species featuring the appropriate set of traits (Keddy 1992; Grime 1997) and leads to shifts in the traits of plant populations (Carroll et al. 2007; Tungate et al. 2007). Changing environmental conditions may favor traits of dominant (e.g., invasive) species, which are able to significantly alter ecosystem function (Wilson and Agnew 1992; Schulze and Mooney 1994).

Here, by the term "trait shift" we refer to visible and measurable alterations of morphological or physiological attributes of individual plant species caused by changes in climatic conditions. Trait shifts mainly become apparent at the population scale and result from natural selection of individuals that perform differently under altered environmental conditions. They are usually caused by changes in the genotype and, hence, represent evolutionary adjustments to the altered environmental conditions (Levin 2009; Lavergne et al. 2010; Richardson et al. 2013). In fragmented populations, climate-mediated trait shifts may result in the formation of climatic ecotypes that fit the local conditions. Trait shifts are a prerequisite to niche shifts and can cause range shifts, if they enable a species to proliferate in areas with different environmental conditions.

As described, trait shifts are often related to phenology, morphology, physiology, and reproduction. In arable land use systems, they do not only occur as a consequence of climatic changes, but also as a result of altered agronomical practice. The adjustment of sowing dates to changing spring and autumn temperature conditions that farmers used to practice in the past decades is relevant in this context (Otte et al. 2006; Chmielewski et al. 2004). For example. the germination temperature range of *Chenopodium ficifolium* as measured in the 1950s was between 30 and 40 °C (Lauer 1953), whereas in the late 1980s, it was between 0 and 30 °C. According to Otte (1991), this trait shift mainly occurred as an adaptation to earlier spring crop sowing dates, which were adopted by farmers during that period of time in Germany. Similar findings were reported for *Chenopodium album* that flowered earlier in northern regions of the UK (Froud-Williams 1996).

S. media, a plant endemic to Central Europe, had originally been restricted to damp, nutrient-rich places around riverbanks (Lohmeyer 1954). The species has adapted some biological traits such as flowering time and germination characteristics to contemporary farming practices (Lososova and Simonova 2008). Evolutionary adjustments such as polyploidy may have occurred in parallel (Rauber 1977). In arable ecosystems, the species now features a larger plasticity regarding both warmer winter conditions and farming practices such as high fertilization. The weed is now able to germinate and flower during the whole year within a larger temperature range (Baessler and Klotz 2006; Fried et al. 2010).

Weeds with a low plasticity regarding emergence temperatures and time of emergence may be exposed to disadvantages with climate change, as future conditions drive the emergence timeframe beyond the optimum considered for the species (Nogues-Bravo 2009; Walck et al. 2011). The inability to shift certain traits is often connected to niche conservatism, which is shown by many specialist and rare species (Wiens and Graham 2005; Lososova et al. 2006; Pearman et al. 2008).

8 Discussion and implications for agronomy and research

Land use, agricultural practice, and abiotic environmental conditions including climate select for certain weed species based on the suitability of their ecophysiological profiles. As a result, they act as filters, which determine the species composition of the arable weed community in a particular site (Pearson and Dawson 2003; Cimalova and Lososova 2009; Navas 2012; Stratonovich et al. 2012). The various filters act at different scales (Fig. 3). Whereas climate and land use mainly act at the landscape scale, agricultural management practices prevalently determine the weed composition at the community scale. Changing climatic conditions influence the properties of the individual filters, for example by altering the availability of resources (e.g., precipitation) or by causing the farmers to implement altered farming practices and to eventually cultivate crops with different attributes (Tanaka and Koike 2011) (Fig. 3). As a consequence, species are eliminated from the community, if their traits are not congruent with the new conditions (Keddy 1992; Diaz et al. 1998; Lavorel and Garnier 2002). Climate change further alters biotic interactions, which influence the realized niches of the species (May and MacArthur 1972; Keddy 1992; Blumenthal and Hufbauer 2007). This leads to (functional) trait shifts, which, in turn, influence the composition of the weed community (Navas 2012). A changing climate can eliminate (e.g., local extinction) or add (e.g., colonization, invasion) species to the local species pool and transform the community composition (Drake 1990; Booth and Swanton 2002). Hence, in the future, agronomy will have to consider the interference of new opportunistic weeds that may replace weed species that were formerly of importance.

For example, in recent years, weeds have increased that show traits related to long-growing seasons (Otte et al. 2006). In former times, the sum of growing degree days was too low to allow seeds of *A. theophrasti* to fully ripen during the growing season in Central Europe (Westerman et al. 2012); longer growing seasons during the past 50 years (Menzel et al. 2006) allowed the species to successfully produce ripe seeds. Climate change involving warmer temperatures will thus

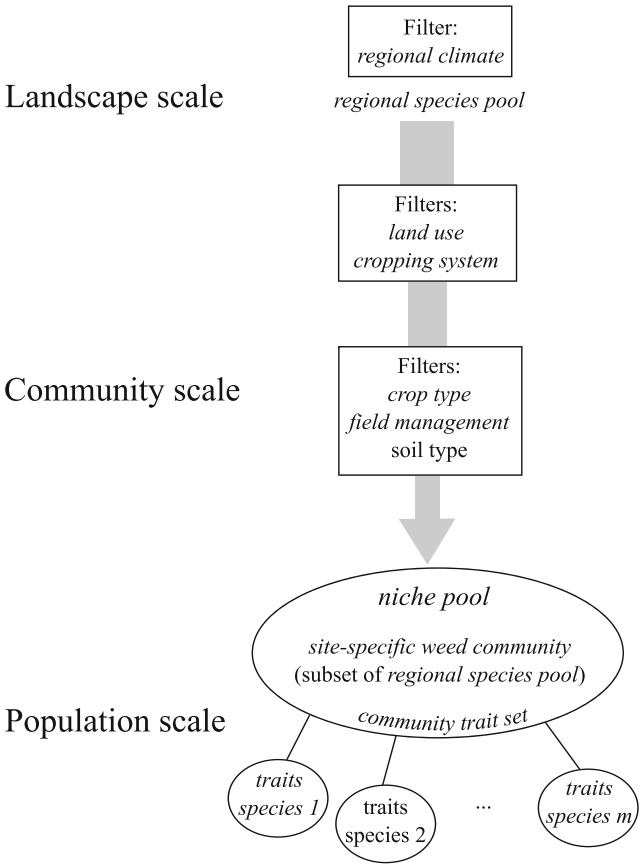

Fig. 3 Filters that determine the arable species composition acting at three distinct scales. Factors as influenced by climate change are shown in *italic font*. Due to climate change, the regional species pool is altered and species are possibly removed and/or added. As a result, the local niche pool will contain a different number of species occupying different niches. Species may have a different trait disposition with climate change. The weed community is site-specific and is also influenced by the sets of traits of the species

allow the species to successfully reproduce and to get established further north in Central Europe.

Among the species that benefit from climate change, there are certainly those that already possess or will develop opportunistic attributes related to climate change. Attributes such as drought and heat tolerance, the C_4 photosynthesis type, the date of first flowering, high seed production, small and light seeds, great dispersal capability, a fast life cycle, and regeneration after disturbance have been identified to be particularly relevant with regard to the predicted future changes. Most of these traits are also beneficial for weeds under intensive and uniform cultivation practices (Hulme 2008). Weeds that benefit from current environmental change often have high phenotypic plasticity with regard to climate. This suggests that a single set of traits that explain the success of certain weed species is unlikely to be found (Richardson and Pysek 2006). With regard to traits related to the exploitation and use of water, climate change will favor weeds that are equipped with the C_4 carbon fixation pathway such as *A. retroflexus* (Lloret et al. 2005; Walther et al. 2009; Gassó et al. 2009) (Fig. 1) and *Echinochloa crus-galli* (Barrett and Wilson 1981; Otte et al. 2006). Wetter and milder winters will increase the survival of some winter annuals such as *S. media* and *Sisymbrium* species that already possess strong traits related to these climate conditions (Walck et al. 2011; Hanzlik and Gerowitt 2012).

Crop management often selects for weeds whose attributes are similar to those of the crop and weeds that are adapted to frequent disturbance typically for intensive practices (Essl et al. 2011). For example, due to the limited specificity of herbicides (Clements et al. 1994; Ziska et al. 1999), crucifer (Brassicaceae) weeds that are closely related to oilseed rape, such as *Sisymbrium* species, *Descurainia sophia*, and *Capsella bursa-pastoris* are nowadays common in fields in Germany (Hanzlik and Gerowitt 2012). In maize cropping, typical weeds appear to be genetically related millets such as *E. crus-galli*, *Setaria* spp., and *Digitaria* spp. (Mehrtens et al. 2005). They seem to be the outcome of short-term selection processes and their presence is mainly caused by modern management practices.

The introduction of arable newcomers as a result of climate-induced range shifts is often facilitated by farming practices and niche gaps (Maillet and Lopez-Garcia 2000), but also depends on the attributes of the resident and invading species (Lavorel et al. 1999; Chapin et al. 2000). Exotics and invaders are range-expanding plants that are at the boundaries of their distribution. These species often show increased adaptive evolutionary responses that enable them to cope with fluctuations better than the resident species (Linhart and Grant 1996; Barrett 2000). Increased disturbance as a result of extreme weather events can additionally act as a driver of trait differentiation in plant communities (Grime 2006; Jauni and Hyvönen 2012) and may already have benefited some alien species such as *Centaurea solstitialis* and *Hypericum maculatum* (Maron et al. 2007; Hierro et al. 2013). Agronomical practice should, therefore, aim at mitigating niche gaps by cultural methods (e.g., crop rotation, sowing time, tillage). Integrated weed management (IWM) combines cultural methods with occasional herbicide use (Anderson 2007). Hence, herbicide use in the IWM concept helps to improve and steer the outcome of cultural control. By contrast, repeated herbicide treatments cause additional and new niche gaps.

As each weed population has its individual set of functional traits, within the community, these traits of several species add up to a "community trait set." By altering the weed species composition, a changing climate thus also alters the disposition and number of trait sets within the community. These processes will influence species niches, as well as agronomy and weed control. When accounting for the impact of climate-mediated shifts on weeds and weed communities, in agronomy, a valuation is performed with regard to the potential damage or yield losses caused by weeds in crops. The term

"damage niche" was shaped to account for the agronomic damage potential of weeds. Accordingly, the term "damage shift" addresses alterations of the damage potential of weeds in particular areas of their distribution against the backdrop of changing environmental conditions (McDonald et al. 2009; Stratonovich et al. 2012) (Table 1). For example, McDonald et al. (2009) modeled the geographical range of the damage niche for the two weed species *A. theophrasti* and *S. halepense* in the USA. With climate change, both species are projected to extend their damage niche further north. The two species are also important maize weeds in Europe (Salonen et al. 2001; Hyvönen 2011). For the UK, yield losses caused by *Alopecurus myosuroides* may be reduced because of climate change (Stratonovich et al. 2012). A more sophisticated understanding of climate-mediated trait shifts and connected niche shifts by measuring attributes of weeds and weed-crop interactions will help to anticipate the possible future damage niches of weeds and to devise management options (Howden et al. 2007; Neve et al. 2009; Gunton et al. 2011; Petit et al. 2011).

Prediction of the future damage niches of weeds is of prevalent importance for a sustainable weed management. In order to assure yields in the face of predicted future conditions and possible extreme weather events, famers may adopt more intensive crop protection practices in the future (Essl et al. 2011). Certain intensive management practices such as the inappropriate use of herbicides at frequent intervals, however, can facilitate the evolution of herbicide resistance in weed populations (Mortensen et al. 2000; Neve et al. 2009). Introgression of genes could be an important component of damage shifts as well, although it has not been intensively studied so far (Sakai et al. 2001; Jump et al. 2008). Regionally explicit predictions of the damage potential caused by weeds in the future may help to devise alternative and additional management options to herbicide treatment. Broader crop rotations for example may help to reduce the pressure from certain weeds.

In order to predict future changes, it is necessary to determine the functional connections between present environmental conditions and species attributes in order to estimate the future relevance of weeds. Besides selected species traits, the weed species composition is an indicator of the occurrence of underlying shifts. Impacts of climate change on arable ecosystems can thus be detected by a continuous monitoring of the weed species composition accompanied by an analysis of further recent transformations. Changes in weed composition result from the combined effects of range transformations, changes in the arrangement and size of niches, and the disposition of functional traits. Therefore, a stronger consideration of trait shifts is needed. The screening of population traits across the distribution range of weeds may support this aim (Petit et al. 2011).

The ability to predict the future damage potential of weeds is strongly related to modeling. With regard to climate change, bioclimatic envelope models (habitat suitability models) are currently widely used to predict the species' response to the altered environmental conditions (Pearson and Dawson 2003; Heikkinen et al. 2006; Fordham et al. 2013). Yet, most current modeling approaches have a limited accuracy as they mainly integrate processes at the landscape scale (Fordham et al. 2013). Most bioclimatic models only consider the fundamental niche of a species rather than the realized niche, which is explained by additional factors at community and population scales (Austin and Van Niel 2011). As a result, there may be a discrepancy between the observed results of experiments and the modeled distribution (Peters and Gerowitt 2014). Especially with rare species and invaders, additional data are needed to accurately estimate the potential for future shifts (Morin and Thuiller 2009; Hulme and Barrett 2013).

9 Conclusions

Shifts are the most important outcome of climate change in arable ecosystems. In agronomy and weed research, processes induced by climate change have, so far, received most interest in comprehensive studies at the landscape scale. We have revealed the influence of processes at other scales, namely niche and trait shifts. Range shifts are investigated with bioclimatic distribution models. As described above, deficiencies at the other scales can be expected to cause inconsistencies between observations and predictions of these models. Thus, knowledge of the underlying processes that lead to trait and niche shifts will probably enhance the prediction accuracy of bioclimatic distribution models when added to those that rely on range shifts. Hence, trait-climate relationships and species interactions warrant closer consideration when modeling the possible future distribution of species (Box 1996; Fordham et al. 2013; Hulme and Barrett 2013).

Currently, little original research is available on niche and trait shifts of arable weeds with regard to climate change. Research approaches on the impacts of climate change on weeds in arable ecosystems need to reflect the functional interrelations and have to take stronger focus on systemic approaches combining process-oriented with spatially explicit investigation. The sole consideration of the individual types of shifts is most unlikely to be sufficient to depict the effects of climate change. A promising option in this respect is to combine species distribution modeling with the monitoring of alterations in the weed species composition and with empirical experiments on weeds under altered conditions (Breitsameter et al. 2014).

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